

HIGH SEEDLING RELATIVE GROWTH RATE AND SPECIFIC LEAF AREA ARE TRAITS OF INVASIVE SPECIES: PHYLOGENETICALLY INDEPENDENT CONTRASTS OF WOODY ANGIOSPERMS¹

EVA GROTKOPP² AND MARCEL REJMÁNEK

Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, California 95616 USA

Understanding causal factors of exotic species invasions is important not only for prevention and prioritizing control efforts, but also for providing valuable insights into the underlying biology of contrasting life-history strategies. In seedling growth analyses, invasive woody species were compared with less-invasive woody species commonly cultivated in California using phylogenetically corrected procedures (12 phylogenetically independent contrasts). Invasive species were hypothesized to have higher seedling relative growth rates (RGRs) and specific leaf areas (SLAs) than did related less-invasive species. In phylogenetically independent contrasts conducted among taxa within families, high seedling RGRs and SLAs have significant positive associations with woody plant invasiveness. For contrasts containing species invasive in mediterranean regions, invasive species had significantly larger root biomass allocation than did less-invasive species. Optimization of fast seedling growth (high RGR) associated with opportunistic resource acquisition (high SLA) and increased root allocation to survive summer drought may be critical for the success of plant invaders in regions with mediterranean climates.

Key words: invasive species; life-history; mediterranean climate; phylogenetically independent contrasts; relative growth rate; root biomass allocation; specific leaf area; woody plants.

Invasive species are those species that establish and spread when introduced beyond their native range (Pyšek et al., 2004). Although few introduced species naturalize and even fewer become invasive, many of those that do become invasive have undesirable ecological, aesthetic, and/or economic impacts (Rejmánek and Pitcairn, 2002; Pimentel et al., 2005; Simberloff, 2005). For example, among the most dangerous invaders in riparian areas in the western United States are several species and hybrids of tamarisks (*Tamarix*). The cost of irrigation water lost to tamarisks has been estimated as between 2 and 7 billion U.S. dollars (Zavaleta, 2000). One of the best-documented plant invaders in Hawaii is the actinorrhizal N fixer *Morella faya*. In N-limited ecosystems of the Hawaii Volcanoes National Park, this species increases the inputs of N from c. 11 to c. 30 kg N·ha⁻¹ (Vitousek, 2004). Some of the N fixed by *Morella* becomes available to other invasive plant species. Similarly, the *Rhizobium*-nodulated invasive shrub, Scotch broom (*Cytisus scoparius*), not only increases N inputs in many places where this is not desirable, but the combined negative effects of this species amount to more than \$11 million annually in western North America (Isaacson, 2000).

Most invasive woody species were introduced for horticultural reasons in the past. Horticulture, via nurseries, seed companies, and botanical gardens, remains the most likely source of new introductions of invasive woody species in the United States (reviewed by Reichard and White, 2001). Predicting which of the many exotic species of potential

horticultural value are invasive when introduced into a new region is an important goal for screening imported species and for prioritizing control of exotic species already introduced into natural areas, especially when little is known about a species' behavior or life-history attributes. While having practical applications, comparative studies of invasive and non-invasive plant species also address some basic ecological questions regarding the underlying biology of contrasting life-history strategies.

There are several well-defined factors contributing to the success of invasive plant species (Rejmánek et al., 2005a), especially in the disturbed habitats that make up most of the modern landscapes (Hannah et al., 1994). Some life-history traits that seem to be particularly important for invasive plant species include fast relative growth rate (Grotkopp et al., 2002; Burns, 2004, 2006) and reproductive and/or dispersal-related traits such as short generation time, small seed mass, short intervals between large seed crops, fruits attractive to vertebrates, and long fruiting periods (Reichard, 1994; Rejmánek and Richardson, 1996; Widrlechner et al., 2004). High specific leaf area (SLA) is a trait that is often associated with a high relative growth rate, small seed mass, and invasiveness (Grotkopp et al., 2002; Lake and Leishman, 2004; Hamilton et al., 2005; Leishman and Thomson, 2005). Due to the associated rapid leaf production, a high SLA allows opportunistic capture of solar energy. Moreover, at least under nonstressful conditions, there seems to be a positive interdependence of plant abilities to forage for light and for soil resources (Donald, 1958; Campbell et al., 1991; Grime, 1993). Opportunistic resource acquisition for growth and reproduction appears to be the key mechanism that makes the aforementioned life-history traits so important for invasive species (Davis et al., 2000; Burns, 2004, 2006; Leishman and Thomson, 2005; Blumenthal, 2005).

Additional traits may be critical for invaders in regions with a mediterranean climate, which are notorious for being invaded by large numbers of exotic plant species (Fig. 13.1 in Rejmánek et al., 2005b). One of these is the ability of

¹ Manuscript received 12 March 2006; revision accepted 21 January 2007.

The authors thank W. Roberts of the UCD Arboretum for his insights and extensive horticultural knowledge that helped us choose species for this study, J. Erskine Ogden for help with harvesting, and C. Aslan, D. Ayres, M. Bower, R. Klinger, R. McKee, and two anonymous reviewers for helpful comments on this manuscript. This work was funded by the USDA-CSREES UC-IPM Exotic/Invasive Pests and Diseases Research Program (Grant #01-34439-10697, Project #01XN020) to M.R.

² Author for correspondence (e-mail: ekgrotkopp@ucdavis.edu)

seedlings to develop extensive root systems quickly before the long, dry summer begins (Hulbert, 1955; Roché et al., 1994). In general, a significant increase in allocation to roots is associated with decreasing precipitation (Mokany et al., 2006).

Seedling relative growth rate (RGR) under nutrient-rich conditions may be the trait that could be used to distinguish invasive species from less-invasive species, considering that much of the modern landscape is the recipient of increased resources due to anthropogenic disturbance and pollution (Vitousek et al., 1997; Blumenthal, 2005). High seedling RGR under optimal conditions was the most important trait associated with invasiveness for pine species (Grotkopp et al., 2002). Similar results recently emerged from near maximum RGR studies of some herbaceous plants under optimal conditions: six species of dayflowers (Commelinaceae) (Burns, 2004, 2006) and four species of *Senecio* (Asteraceae) (Garcia-Serrano et al., 2005). In contrast, Bellingham et al. (2004) found no relationship between invasiveness and RGR for seedlings of 33 woody species of gymnosperms and angiosperms.

Seedling relative growth rate analysis is a powerful tool for understanding life-history traits because it combines aspects of species' anatomy, morphology, and physiology (Grotkopp et al., 2002). Classic growth analysis decomposes RGR into two components: net assimilation rate (NAR) and leaf area ratio (LAR). Furthermore, LAR can be decomposed into leaf mass ratio (LMR) and specific leaf area (SLA) (Causton and Venus, 1981; Hunt, 1982):

$$\text{RGR}(\text{mg} \cdot \text{g}_{\text{plant}}^{-1} \cdot \text{d}^{-1}) = \text{NAR}(\text{mg} \cdot \text{cm}_{\text{leaf}}^{-2} \cdot \text{d}^{-1}) \cdot \text{LAR}(\text{cm}_{\text{leaf}}^2 \cdot \text{g}_{\text{plant}}^{-1})$$

$$\text{LAR}(\text{cm}_{\text{leaf}}^2 \cdot \text{g}_{\text{plant}}^{-1}) = \text{LMR}(\text{g}_{\text{leaf}} \cdot \text{g}_{\text{plant}}^{-1}) \cdot \text{SLA}(\text{cm}_{\text{leaf}}^2 \cdot \text{g}_{\text{leaf}}^{-1})$$

Here, using 28 species, we tested the hypothesis that invasive woody angiosperms have faster seedling relative growth rates and higher specific leaf areas than do less-invasive woody angiosperms. In addition, we ask whether invasive woody species successful in mediterranean climates have a greater biomass allocation to roots than less-invasive species. The species used in this study were exotic horticultural plants that have been cultivated successfully in California for many years but differ in their degrees of invasiveness. In this way, we minimized differences in human introduction effort that can confound analyses of invasive and non-invasive species (Bellingham et al., 2004). We also avoided comparing exotics (only a small percentage of which are invasive) with natives (some of which may be invasive when introduced beyond their native range) (Rejmánek, 1999; Muth and Pigliucci, 2006). Finally, and most importantly, we analyzed sets of taxonomically related species contrasting in their invasiveness to detect trends that may otherwise be unapparent in across-species analyses. In other words, by using phylogenetically independent contrasts, we took shared phylogeny into account and only looked at differences between invasive and non-/less-invasive species within a clade (Felsenstein, 1985; Harvey and Pagel, 1991; Ackerly, 1999).

MATERIALS AND METHODS

Species selection and invasiveness status—The species used in this study (see Table 1) were limited to exotic woody plants (with the exception of *Fraxinus velutina*, which is native in southern California) that have been commonly planted in California for at least 100 years. They are included in *The*

Sunset Western Garden Book (Brenzel, 2001) and in older books on cultivated ornamentals in California (Hall, 1910; Saunders, 1926; Wilson, 1938; Graham and McMinn, 1941). Species selection was based on theoretical as well as practical considerations. Our goal was to pair species that differed mainly in invasiveness. We tried to contrast invasive species with phylogenetically related non-invasive species (or, if not possible, with related much less-invasive species) that were similar in growth habit, leaf habit (evergreen/deciduous), seed dispersal mode, flower color, and aesthetics. We consulted with horticultural and invasive species experts (W. Roberts, University of California-Davis Arboretum, and J. Randall, Nature Conservancy, personal communications) to find the most similar species. For the final selection, we used species that had available seeds, either commercially or from local specimens. Most of the invasive species chosen are considered as invasive in mediterranean regions. However, included were also a few species invasive in mesic areas (in the *Rosa* and *Acer* contrasts). For the purposes of our analyses, “invasive species” were those species that, based on available data, can be classified as “invasive” (sensu Pyšek et al., 2004; i.e., regenerating ≥ 100 m from source trees in less than 50 yr) in California or that have been reported as clearly invasive in other states or regions in the world, mainly based on data in Randall (2002) and Weber (2003). “Less-invasive species” were those species that, in spite of widespread planting, have never been reported as invasive in California or anywhere else in the world or that have only limited, local reproduction. To illustrate the utilization of data available in the literature, the information available for *Acacia dealbata* (invasive) and *A. pendula* (less/non-invasive) in Randall's (2002) compendium of weeds can be used as an example. The first species, based on 26 references, is classified as a naturalized, noxious, and environmental weed. The second species is just classified as “introduced” and the single reference points to the Kew Royal Botanic Gardens database Survey of Economic Plants for Arid and Semi-Arid Lands (available at <http://www.rbgekew.org.uk/ceb/sepsal/>). Pairs or groups of related invasive and less-invasive species were chosen to form phylogenetically independent contrasts (Table 1). Intergeneric contrasts within Fabaceae were constructed based on the phylogeny of Wojciechowski et al. (2004). In two cases we could not find a suitable contrast within a family and therefore constructed interfamilial contrasts, using species from phylogenetically related families (Table 1). In total, we planted 35 species for 15 sets of phylogenetically independent contrasts to test the hypotheses that invasive species have higher relative growth rates and higher specific leaf areas than less-invasive species. However, due to poor germination of four species and the uncertain invasiveness status of two species, we could only analyze 12 contrasts, consisting of data from 26 species, for the 10 to 30 d growth interval. Despite low germination, we were able to harvest five seedlings of *Rosa glauca* at 30 d and therefore have the additional *Rosa* (two species) contrast for an analysis from seed to 30 d.

Seeds, stratification, and planting—Seeds were either collected (from one to 10 mother plants) or ordered from seed companies (Carter Seeds, Vista, California, USA and Sheffield's Seed Co., Locke, New York, USA). At least 30 randomly chosen air-dried seeds were weighed for each species to calculate the mean seed mass. Seeds were surface sterilized with 1% sodium hypochlorite solution for 3–5 min, rinsed extensively, and then stratified and/or scarified according to the directions of the seed company. Pots (164 mL volume SC-10 Super Cell, Stuewe and Sons, Corvallis, Oregon, USA) were filled with sterilized UC Mix (25% Canadian sphagnum peat, 25% uniform coarse sand, 25% white pumice, 25% redwood compost with the following added per cubic meter (approximately 26.7 kg dry): 1.8 kg oyster lime, 1.8 kg dolomite 65, 1.8 kg single super phosphate. The soil was saturated with diluted nutrient solution (N : P : K = 202 : 72 : 152 ppm made from 0.5% GrowMore 4-18-38 No Boron, National Research and Chemical, Gardena, California, USA, with solution-grade calcium nitrate added). Seeds were sown in late winter 2004 at depths recommended for each species. Two pots of each species were randomly arranged on each of 15 trays, for a total of 30 pots/species. The date that each seedling emerged above the soil level was recorded, and plants were thinned randomly to one per pot by 5–7 d after seedling emergence.

Growth conditions—All pots were allowed to dry out at the surface and then lightly watered every day, alternating distilled water and dilute nutrient solution (as described). Mean minimum and maximum temperatures were 15.0°C and 28.6°C, respectively. Because the greenhouse we used was a shared facility, high pressure sodium lamps were on to supplement natural daylight to 16 h light/day.

TABLE 1. Phylogenetically independent contrasts used in this study, the species used to construct them, species' relative level of invasiveness, habit (E = evergreen, D = deciduous), dispersal mode, and native distribution.

Contrast	Species	Invasiveness	Habit	Dispersal mode	Native distribution
Fabaceae 1	<i>Acacia dealbata</i> Link	more	E tree	myrmecochory	SE Australia
	<i>Acacia pendula</i> A. Cunn ex G. Don	less	E tree	myrmecochory	E Australia
Fabaceae 2	<i>Cytisus scoparius</i> (L.) Link	more	D/E shrub	ballistic/myrmecochory	W Europe
	<i>Genista monspessulana</i> (L.) L.A.S. Johnson	more	E shrub	ballistic/myrmecochory	W Europe
Fabaceae 3	<i>Genista aethnensis</i> DC.	less	D shrub	myrmecochory	Italy
	<i>Albizia julibrissin</i> Durazz.	more	D tree	gravity/wind	Iran to Japan
Fabaceae 4	<i>Ceratonia siliqua</i> L.	less	E tree	endozoochory	S Europe
	<i>Robinia pseudoacacia</i> L.	more	D tree	wind/gravity	SE USA
Moraceae	<i>Sesbania punicea</i> (Cav.) Benth.	more	D tree	water	Argentina, Brazil
	<i>Cercis canadensis</i> L.	less	D tree	bird	E, midwest USA
	<i>Ficus carica</i> L.	more	D tree	endozoochory	S Europe, SW Asia
Sapindaceae	<i>Maclura pomifera</i> (Raf.) C.K. Schneid.	less	D tree	endozoochory	USA: OK, AR, TX
	<i>Acer ginnala</i> Maxim.	more	D tree	wind	E Asia
Rosaceae 1	<i>Acer truncatum</i> Bunge	less	D tree	wind	China
	<i>Cotoneaster lacteus</i> W.W. Sm.	more	E shrub	endozoochory	S China
Rosaceae 2	<i>Photinia serrulata</i> Lindl.	less	E shrub	endozoochory	E Asia
	<i>Rubus armeniacus</i> Focke	more	D/E shrub	endozoochory	Caucasia
Rosaceae 3	<i>Rubus idaeus</i> L.	less	D shrub	endozoochory	circumboreal
	<i>Rosa multiflora</i> Thunb. ex Murr.	more	D shrub	endozoochory/gravity	E Asia
Myrtaceae	<i>Rosa glauca</i> Pourr.	less	D shrub	endozoochory	Europe
	<i>Eucalyptus camaldulensis</i> Dehnh.	more	E tree	censer	Australia
Oleaceae	<i>Eucalyptus leucoxylon</i> F. Muell.	less	E tree	censer	Australia
	<i>Fraxinus velutina</i> Torr.	more	D tree	wind	SW USA, Mexico
Simaroubaceae/	<i>Syringa vulgaris</i> L.	less	D shrub	censer	S Europe
	<i>Ailanthus altissima</i> (Mill.) Swingle	more	D tree	wind	N China, E Asia
Meliaceae	<i>Toona sinensis</i> (Juss.) M.J. Roem.	less	D tree	wind	China
Myrtaceae/	<i>Metrosideros excelsa</i> Sol. ex Gaertn.	more	E tree	censer	New Zealand
Lythraceae	<i>Lagerstroemia indica</i> L.	less	D tree	censer	China

Harvesting—An average of 10 plants were randomly harvested for most species at 10, 20, and 30 d after seedling emergence, which was recorded for each individual. For five species (*Acer ginnala*, *Fraxinus velutina*, *Robinia pseudoacacia*, *Rosa glauca*, and *Sesbania punicea*), fewer plants (average of six plants/harvest) were harvested due to low germination rates. Pots were cut open, the seedlings carefully removed, and the roots washed. The leaves of each harvested plant were photographed with a digital camera to calculate total leaf area using the public domain NIH Image 1.61 program (developed at the U.S. National Institutes of Health, available at <http://rsb.info.nih.gov/nih-image/>). Roots, cotyledons, leaves, and shoots were placed into separate envelopes and placed into a drying oven at 70°C for 48 h. Dry biomass was weighed to the nearest 0.1 mg with an analytical balance.

Growth analysis—Relative growth rate (RGR) and net assimilation rate (NAR) and their variances were calculated for the intervals 10 to 20 d and 10 to 30 d after emergence according to the formulae from Causton and Venus (1981) for ungraded and unpaired harvests. The interval from 10 to 30 d was used for most analyses because this longer time encompassed more environmental fluctuations within the greenhouse. Leaf area ratio (LAR), leaf mass ratio (LMR), and specific leaf area (SLA) were quantified at the midpoint (20 d) of the growth interval from 10 to 30 d. For the growth interval from 10 to 20 d, these quantities were estimated as the average of the data from 10 d and from 20 d. RGR was also measured for the interval 0 (seed mass as initial mass) to 30 d to include the *Rosa* contrast (as described earlier). Growth analyses were performed using both total and aboveground biomass for the interval from 10 to 30 d. Biomass allocation to roots was calculated at 30 d.

Statistical analysis—Data were compared between invasive and less-invasive species using phylogenetically corrected analyses. If more than one species were used for half of a phylogenetically independent contrast, their values were averaged. Data for proportion of root biomass were analyzed after arc sine angular transformation ($\sin^{-1}\sqrt{X}$). One-tailed paired *t* tests were conducted with StatView 5.0.1 (SAS Institute, 1998).

RESULTS

Growth analysis—Relative growth rate (RGR) varied from 39 $\text{mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ for the less-invasive *Ceratonia siliqua* to 215 $\text{mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ for the invasive *Eucalyptus camaldulensis* (Table 2). The lowest specific leaf areas (SLA), 101 $\text{cm}^2\cdot\text{g}^{-1}$ and 103 $\text{cm}^2\cdot\text{g}^{-1}$, were those of the less-invasive species *C. siliqua* and *Acacia pendula*, respectively, while the highest SLAs (315 $\text{cm}^2\cdot\text{g}^{-1}$ and 295 $\text{cm}^2\cdot\text{g}^{-1}$) were again from invasive species, *E. camaldulensis* and *Rubus armeniacus*, respectively (Table 2).

Analyses of phylogenetically independent contrasts—Paired *t* tests with all phylogenetically independent contrasts ($N = 12$) for the interval 10 to 30 d showed that invasive species did not have significantly higher values than less-invasive species for most quantities measured [NAR, LAR, SLA, LMR, and $\log(\text{seed mass})$], although RGR was marginally significantly different (Tables 2, 3). However, when the two interfamilial contrasts were omitted from the analysis to avoid larger phylogenetic distances, both RGR and SLA were significantly higher for the invasive species (Table 3). Results were consistent when the data from 10 to 20 d were analyzed (data not shown). For the interval 0 (seed mass) to 30 d, which included the *Rosa* contrast, RGR was significantly higher for invasive species when the two interfamilial contrasts were omitted (one-tailed paired *t* test, $N = 11$, $P = 0.029$), but not when all contrasts were included (one-tailed paired *t* test, $N = 13$, $P = 0.106$). Percentage biomass allocation to roots was not significantly different for all contrasts or for only intrafamilial contrasts (one-tailed paired *t* tests, both $P > 0.112$). However, when contrasts with invaders in primarily mesic areas were

TABLE 2. Contrasts and the species used to construct them, along with species' relative level of invasiveness, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf mass ratio (LMR), and specific leaf area (SLA), in addition to percentage root biomass at 30 d after emergence and mean seed mass. All growth analysis components are means (\pm SE) from the interval 10–30 d after emergence.

Contrast	Species	Invasiveness	RGR (mg·g ⁻¹ ·d ⁻¹)	NAR (mg·cm ⁻² ·d ⁻¹)	LAR (cm ² ·g ⁻¹)	LMR (g _{leaf} ·g ⁻¹)	SLA (cm ² _{leaf} ·g ⁻¹)	Root mass (%)	Mean seed mass (mg)
Fabaceae 1	<i>Acacia dealbata</i>	more	79.3 (6.6)	0.7 (1.0)	103.2 (8.6)	0.541 (0.018)	189.5 (11.5)	35.9 (1.6)	14.0
	<i>Acacia pendula</i>	less	80.2 (6.6)	1.2 (1.4)	58.6 (4.0)	0.567 (0.015)	103.3 (5.8)	38.1 (1.8)	24.0
Fabaceae 2	<i>Cytisus scoparius</i>	more	69.5 (6.4)	0.9 (2.0)	78.5 (5.9)	0.540 (0.018)	146.9 (13.4)	36.2 (1.4)	8.0
	<i>Genista monspessulana</i>	more	65.3 (8.0)	0.8 (3.5)	85.1 (4.5)	0.571 (0.010)	148.9 (7.3)	41.0 (2.2)	7.5
Fabaceae 3	<i>Genista aethnensis</i>	less	76.7 (4.9)	1.3 (3.2)	81.7 (5.0)	0.469 (0.013)	174.4 (9.9)	46.0 (1.5)	9.6
	<i>Albizia julibrissin</i>	more	78.4 (5.2)	0.7 (0.4)	139.6 (10.2)	0.541 (0.011)	257.5 (15.1)	42.0 (1.2)	45.0
Fabaceae 4	<i>Ceratonia siliqua</i>	less	38.7 (3.3)	0.7 (0.3)	68.1 (3.2)	0.676 (0.007)	101.0 (5.2)	20.8 (1.2)	187.1
	<i>Robinia pseudoacacia</i>	more	101.2 (15.6)	0.8 (0.4)	147.1 (12.0)	0.605 (0.007)	243.1 (18.9)	34.4 (1.7)	22.8
Moraceae	<i>Sesbania punicea</i>	more	93.2 (14.4)	1.4 (0.9)	78.1 (5.1)	0.482 (0.019)	162.8 (11.5)	37.5 (3.0)	69.9
	<i>Cercis canadensis</i>	less	82.3 (3.4)	0.6 (0.3)	132.7 (8.2)	0.684 (0.008)	194.1 (6.3)	22.6 (1.0)	32.2
	<i>Ficus carica</i>	more	154.8 (7.1)	1.2 (0.9)	117.0 (8.0)	0.532 (0.013)	220.2 (14.8)	39.0 (1.4)	1.0
Sapindaceae	<i>Maclura pomifera</i>	less	84.4 (5.4)	1.0 (0.3)	93.6 (2.9)	0.588 (0.006)	159.4 (4.8)	26.6 (0.7)	53.3
	<i>Acer ginnala</i>	more	103.4 (7.4)	0.6 (0.3)	215.8 (11.1)	0.642 (0.008)	336.9 (18.9)	25.8 (1.9)	15.2
Rosaceae 1	<i>Acer truncatum</i>	less	94.7 (5.7)	0.7 (0.1)	113.4 (6.9)	0.541 (0.013)	209.8 (12.7)	34.8 (2.0)	122.6
	<i>Cotoneaster lacteus</i>	more	125.5 (3.1)	1.5 (0.7)	90.5 (2.4)	0.610 (0.007)	148.5 (3.6)	37.7 (1.0)	6.8
Rosaceae 2	<i>Photinia serrulata</i>	less	101.8 (5.8)	0.8 (1.7)	151.4 (5.5)	0.695 (0.017)	219.8 (11.4)	16.5 (0.7)	4.0
	<i>Rubus armeniacus</i>	more	160.4 (9.9)	1.1 (0.5)	180.6 (9.8)	0.621 (0.038)	295.4 (17.4)	40.8 (1.7)	2.6
Rosaceae 3	<i>Rubus idaeus</i>	less	186.6 (13.5)	1.2 (0.8)	142.7 (5.3)	0.550 (0.018)	261.2 (11.1)	40.7 (1.2)	1.1
	<i>Rosa multiflora</i>	more	112.3 ^a	—	—	—	—	34.3 (1.5)	6.9
Myrtaceae	<i>Rosa glauca</i>	less	45.2 ^a	—	—	—	—	40.2 (2.3)	15.5
	<i>Eucalyptus camaldulensis</i>	more	214.9 (9.2)	1.7 (0.4)	161.3 (9.0)	0.510 (0.019)	315.6 (11.7)	35.7 (2.1)	0.5
Oleaceae	<i>Eucalyptus leucoxylon</i>	less	142.6 (7.7)	1.5 (1.5)	129.6 (3.2)	0.583 (0.016)	223.6 (6.8)	36.7 (1.7)	0.5
	<i>Fraxinus velutina</i>	more	87.8 (10.4)	1.0 (1.9)	98.7 (9.3)	0.472 (0.014)	209.3 (19.5)	42.8 (1.9)	12.3
Simaroubaceae/	<i>Syringa vulgaris</i>	less	51.4 (7.3)	0.6 (6.2)	91.9 (7.1)	0.527 (0.028)	173.8 (7.9)	41.3 (2.7)	5.0
	<i>Ailanthus altissima</i>	more	93.0 (5.0)	0.8 (0.3)	118.5 (4.1)	0.610 (0.010)	194.7 (7.1)	38.1 (1.6)	24.6
Meliaceae	<i>Toona sinensis</i>	less	119.0 (10.4)	0.8 (0.4)	174.3 (6.6)	0.600 (0.010)	290.7 (11.2)	33.5 (2.6)	9.7
Myrtaceae/	<i>Metrosideros excelsa</i>	more	89.6	0.6	121.7	0.609	200.0	25.6	0.1
Lythraceae	<i>Lagerstroemia indica</i>	less	113.4 (9.1)	0.8 (0.7)	174.7 (8.5)	0.634 (0.020)	279.7 (18.8)	28.1 (0.9)	1.8

^a RGR was measured for the interval 0 d (mean seed mass as initial mass) to 30 d after emergence.

excluded (*Acer* and *Rosa*), percentage biomass allocation to roots was significantly greater for invasive species than for less-invasive species, both for all remaining contrasts and for all remaining intrafamilial contrasts (one-tailed, paired *t* tests, *P* = 0.044 and *P* = 0.048, respectively).

TABLE 3. *P* values of comparisons of growth variables, percentage root biomass, and log(seed mass) using one-tailed paired *t* tests of phylogenetically independent contrasts of more-invasive and less-invasive species. More-invasive species were hypothesized to have higher means than less-invasive species of all growth variables and smaller means for log(seed mass). Data are shown for relative growth rate (RGR) and net assimilation rate (NAR) for the interval from 10 to 30 d after emergence, while data for leaf area ratio (LAR), specific leaf area (SLA), and leaf mass ratio (LMR) are shown at the midpoint of the growth interval, 20 d. *P* values smaller than 0.05 are in boldface.

Variable	Total biomass		Aboveground biomass	
	All contrasts <i>N</i> = 12	Intrafamilial contrasts only <i>N</i> = 10	All contrasts <i>N</i> = 12	Intrafamilial contrasts only <i>N</i> = 10
RGR (mg·g ⁻¹ ·d ⁻¹)	0.082	0.026	0.109	0.034
NAR (mg·cm ⁻² ·d ⁻¹)	0.369	0.300	0.666	0.558
LAR (cm ² ·g ⁻¹)	0.243	0.069	0.135	0.019
SLA (cm ² ·g _{leaf} ⁻¹)	0.139	0.024	0.138	0.024
LMR (g _{leaf} ·g ⁻¹)	0.866	0.853	0.663	0.558
Root biomass (%)	0.112 ^a	0.121 ^b		
Log(seed mass)	0.078 ^a	0.106 ^b		

^a *N* = 13, ^b *N* = 11.

DISCUSSION

RGR and SLA as predictors of invasive species—Using intrafamilial phylogenetically independent contrasts, we found that both RGR and SLA were significantly higher for invasive species than for less-invasive species (Tables 2, 3). This is in agreement with our results for *Pinus* (Grotkopp et al., 2002) and with recent results for herbaceous plants in Commelinaceae under high nutrient conditions (Burns, 2004, 2006) and in *Senecio* (Garcia-Serrano et al., 2005). However, Bellingham et al. (2004) in their study of 33 exotic woody species across four families in New Zealand did not find any association between seedling RGR and invasiveness. It should be stressed that different definitions of invasiveness could contribute to the differing results: Bellingham et al. (2004) quantified the actual rate of spread of species already naturalized in New Zealand and used that as a measure of invasiveness (therefore no clearly non-invasive species were considered, with the possible exception of *Pinus uncinata*), while Grotkopp et al. (2002) and we in this study used a qualitative classification of invasiveness status based on the number and severity of worldwide reports (a combination of the number of naturalization events and the extent of spread).

However, we also suggest that Bellingham et al.'s (2004) experimental results are difficult to interpret because they did not measure near maximum seedling RGR under optimal conditions, but the RGR of stressed plants in small pots over a much later growth interval, 11–18 mo. Relative growth rates are near maximal when seedlings are young and then decrease

over time (Causton and Venus, 1981; Hunt, 1982), and differences in RGR between species are most apparent when they are grown under optimal conditions; plants grow slower under lower nutrient levels, and the resultant differences in RGR between species are therefore much less or nonexistent (Burns, 2004). Under the conditions reported in Bellingham et al. (2004), it is not unexpected that differences in relative growth rate among species were not observed. In fact, many of the RGRs reported in their study are negative in the control treatments, as well as in the fertilizer addition treatment.

Despite the significance of the association of high RGR and high SLA with invasiveness in the present analysis, the results are not as clear as they were in our previous study of 29 *Pinus* species (Grotkopp et al., 2002). Several reasons may account for this. First, *Pinus* is a much more homogenous group in terms of physiology, life forms, and reproductive attributes than a broad selection of species across several angiosperm families with varying life forms and dispersal modes (Table 1). Second, the level of invasiveness for many *Pinus* species was more reliably assessed because pines have been very well studied and extensively planted throughout the world (Richardson and Rejmánek, 2004). In contrast, the species used in this study were not always clearly invasive vs. clearly non-invasive. Although invasive species were always paired with related species that were much less invasive, the differences in invasiveness within contrasts varied (due to the level of current knowledge and the constraints of the available species pool). Third, phylogenetic distances varied considerably more here than in the study of *Pinus*, which was restricted to one genus (Grotkopp et al., 2002). We tried to construct phylogenetically independent contrasts within genera and if not possible, then within families. However, in two cases (for *Ailanthus altissima* and for *Metrosideros excelsa* and their respective less-invasive counterparts), we were forced to construct interfamilial contrasts with closely related families. However, these contrasts with large phylogenetic distances turned out to likely be a source of noise in the data (Table 3). Contrasts are best constructed with closely related species, preferably within genera or, at least, within monophyletic families, to minimize phylogenetic effects.

Although both RGR and SLA were almost equally good predictors of invasiveness (Table 3), they were not always in agreement (Table 2). For example, SLA was more closely associated with invasiveness than RGR for *Acacia* and *Acer*, while RGR was more tightly associated with invasiveness for the Rosaceae 1 contrast (Table 2). Several researchers have concluded that leaf traits (including SLA) are often tightly connected to the continuum of life-history traits (Westoby, 1998; Reich et al., 1999; Wright et al., 2004). In many relative growth rate studies, SLA was the major contributing factor (via LAR) in determining RGR (Saverimuttu and Westoby, 1996; Lambers et al., 1998; but see Shipley, 2006). High SLA was associated with exotic invasive species by Baruch and Goldstein (1999) and by Lake and Leishman (2004); however, it is unknown how RGR was related to invasiveness because RGR was not measured in either study. High SLA, LAR, and RGR were significantly associated with invasiveness in *Pinus* (Grotkopp et al., 2002).

In some cases, however, RGR may be a better indicator of invasiveness than SLA. For example, for *Senecio* species, RGR was related to invasiveness while SLA was not (García-Serrano et al., 2005). In a study of five invasive species and four native (and presumably non-invasive) species in Hawaii, Pattison et

al. (1998) found that invasive species had higher RGR than native species due to higher NAR (while LAR were similar) under high light and partial shade. Long-term evolutionary adaptations of individual taxa to environmental conditions are likely responsible for differences in the physiological, anatomical/morphological, and allocational contributions to RGR.

Critical attributes of species invasive in mediterranean climates—Although we found RGR and SLA to be significantly associated with invasiveness, LAR and LMR were not (Table 3). A very important point emerges from this result. While high SLA and RGR seem to contribute to successful invasion of species that are introduced outside their native ranges, long summer drought poses a barrier in regions that have mediterranean climates. For species to successfully invade, they must first have characteristics that allow them to grow quickly and acquire resources opportunistically (high RGR and high SLA, respectively). Additionally, a successful invader must pass through an environmental “filter” of summer drought. These successful invaders must optimize or balance fast seedling growth and opportunistic resource acquisition (RGR and SLA, respectively) with increased allocation to roots for survival over the long, dry summer. Analysis of phylogenetically independent contrasts containing invasive species that are invaders of areas with mediterranean climates shows that these species have larger allocations to roots than do their less-invasive counterparts. This increase in biomass allocation to roots explains the nonsignificance of LAR in our study, because it necessarily decreases LMR and hence, LAR. However, when analyzing only the aboveground biomass, RGR and SLA remain highly significantly associated with invasiveness, and LAR also becomes highly significantly associated with invasiveness (Table 3).

We also did not find that small seed mass was significantly associated with invasiveness (Table 3), in contrast to Rejmánek and Richardson (1996) and Grotkopp et al. (2002). We suggest that this is due to the fact that the majority of the invasive species utilized in this study are invasive in dry mediterranean climates. Jurado and Westoby (1992) found that larger seed size, while not necessarily contributing to a greater root allocation, was an asset for seedling survival in Australian arid areas due to the additional resources packed in the seed. Again, for successful invaders, there appears to be an optimization of fast growth (usually associated with small seeds) and resource capture together with seedling survival in mediterranean climates.

Conclusions—Three major points emerge from this study. First, both high seedling relative growth rate (RGR) and specific leaf area (SLA) are related to woody plant invasiveness. However, the biological basis of this association is still not clear, and detailed studies of causal networks underlying such relationships are badly needed (see Fig. 12 in Grotkopp et al., 2002 and Fig. 5 in Grotkopp et al., 2004). Both RGR and SLA play key roles in capturing available resources. The ability to opportunistically capture resources seems to be the most important in many, if not all, successful cases of plant invasions (Davis et al., 2000; Shea and Chesson, 2002). Second, species invasive in regions with a mediterranean climate had a greater allocation to root biomass than less-invasive species, and this may be an important trait for successful invaders to survive through a mediterranean

summer. Third, the procedures in this study may seem demanding for screening for invasive species. However, unless we know that a species is invasive somewhere else, there are no shortcuts in the evaluation of potential invaders. Comparative seedling growth analysis with related species is certainly not a silver bullet, but it still can be helpful under certain circumstances such as selection from several congeners. Further studies of this kind, testing many more contrasts, will elucidate the usefulness of this approach in screening for invasive species in the horticultural trade as well as in understanding differences in life-history patterns.

LITERATURE CITED

- ACKERLY, D. D. 1999. Comparative plant ecology and the role of phylogenetic information. In M. C. Press, J. D. Scholes, and M. G. Barker [eds.], *Physiological plant ecology*, 391–413. Blackwell Science, Oxford, UK.
- BARUCH, Z., AND G. GOLDSTEIN. 1999. Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia* 121: 183–192.
- BELLINGHAM, P. J., R. P. DUNCAN, W. G. LEE, AND R. P. BUXTON. 2004. Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. *Oikos* 106: 308–316.
- BLUMENTHAL, D. 2005. Interrelated causes of plant invasion. *Science* 310: 243–244.
- BRENZEL, K. N. [ED.]. 2001. *Sunset western garden book*. Sunset Publishing, Menlo Park, California, USA.
- BURNS, J. H. 2004. A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. *Diversity and Distributions* 10: 387–397.
- BURNS, J. H. 2006. Relatedness and environment affect traits associated with invasive and noninvasive introduced Commelinaceae. *Ecological Applications* 16: 1367–1376.
- CAMPBELL, B. D., J. P. GRIME, AND J. M. L. MACKEY. 1991. A trade-off between scale and precision in resource foraging. *Oecologia* 87: 532–538.
- CAUSTON, D. R., AND J. C. VENUS. 1981. *The biometry of plant growth*. Edward Arnold, London, UK.
- DAVIS, M. A., J. P. GRIME, AND K. THOMPSON. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.
- DONALD, C. M. 1958. The interaction of competition for light and for nutrients. *Australian Journal of Agricultural Research* 9: 421–432.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.
- GARCIA-SERRANO, H., J. ESCARRÉ, E. GARNIER, AND F. X. SANS. 2005. A comparative growth analysis between alien invader and native *Senecio* species with distinct distribution ranges. *Ecoscience* 12: 35–43.
- GRAHAM, E., AND H. E. McMINN. 1941. *Ornamental shrubs and woody vines of the Pacific coast*. Gillick Press, Berkeley, California, USA.
- GRIME, J. P. 1993. Stress, competition, resource dynamics and vegetation processes. In L. Fowden, T. Mansfield, and J. Stoddart [eds.], *Plant adaptation to environmental stress*, 45–63. Chapman and Hall, London, UK.
- GROTKOPP, E., M. REJMÁNEK, AND T. L. ROST. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159: 396–419.
- GROTKOPP, E., M. REJMÁNEK, M. J. SANDERSON, AND T. L. ROST. 2004. Evolution of genome size in pines (*Pinus*) and its life-history correlates: supertree analyses. *Evolution* 58: 1705–1729.
- HALL, H. M. 1910. *Studies in ornamental trees and shrubs*. University of California Publications in Botany 4: 1–74.
- HAMILTON, M. A., B. R. MURRAY, M. W. CADOTTE, G. C. HOSE, A. C. BAKER, C. J. HARRIS, AND D. LICARI. 2005. Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* 8: 1066–1074.
- HANNAH, L., D. LOHSE, C. HUTCHINSON, J. L. CARR, AND A. LAKERANI. 1994. A preliminary inventory of human disturbance of world ecosystems. *Ambio* 23: 246–250.
- HARVEY, P. H., AND M. D. PAGEL. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- HULBERT, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. *Ecological Monographs* 25: 181–213.
- HUNT, R. 1982. *Plant growth curves: the functional approach to plant growth analysis*. Thomson Litho, East Kilbride, Scotland.
- ISAACSON, D. L. 2000. Impacts of broom (*Cytisus scoparius*) in western North America. *Plant Protection Quarterly* 15: 145–148.
- JURADO, E., AND M. WESTOBY. 1992. Seedling growth in relation to seed size among species of arid Australia. *Journal of Ecology* 80: 407–416.
- LAKE, J. C., AND M. R. LEISHMAN. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117: 215–226.
- LAMBERS, H., F. S. CHAPIN III, AND T. L. PONS. 1998. *Plant physiological ecology*. Springer, New York, New York, USA.
- LEISHMAN, M. R., AND V. P. THOMSON. 2005. Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. *Journal of Ecology* 93: 38–49.
- MOKANY, K., R. J. RAISON, AND A. S. PROKUSHKIN. 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biology* 12: 84–96.
- MUTH, N. Z., AND M. PIGLIUCCI. 2006. Traits of invasives reconsidered: phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. *American Journal of Botany* 93: 188–196.
- PATTISON, R. R., G. GOLDSTEIN, AND A. ARES. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* 117: 449–459.
- PIMENTEL, D., R. ZUNIGA, AND D. MORRISON. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.
- PYŠEK, P., D. M. RICHARDSON, M. REJMÁNEK, G. L. WEBSTER, M. WILLIAMSON, AND J. KIRSCHNER. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143.
- RANDALL, R. P. 2002. *A global compendium of weeds*. R. G. and F. J. Richardson, Melbourne, Australia.
- REICH, P. B., D. S. ELLSWORTH, M. B. WALTERS, J. M. VOSE, C. GRESHAM, J. C. VOLIN, AND W. D. BOWMAN. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- REICHARD, S. H. 1994. *Assessing the potential of invasiveness in woody plants introduced in North America*. Ph.D. dissertation, University of Washington, Seattle, Washington, USA.
- REICHARD, S. H., AND P. WHITE. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103–113.
- REJMÁNEK, M. 1999. Invasive plant species and invulnerable ecosystems. In O. T. Sandlund, P. J. Schei, and A. Viken [eds.], *Invasive species and biodiversity management*, 79–102. Kluwer, Dordrecht, Netherlands.
- REJMÁNEK, M., AND M. J. PITCAIRN. 2002. When is eradication of exotic pest plants a realistic goal? In C. R. Veitch and M. N. Clout [eds.], *Turning the tide: the eradication of invasive species*, 249–253. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- REJMÁNEK, M., AND D. M. RICHARDSON. 1996. What attributes make some plant species more invasive? *Ecology* 77: 1655–1661.
- REJMÁNEK, M., D. M. RICHARDSON, S. I. HIGGINS, M. J. PITCAIRN, AND E. GROTKOPP. 2005a. Ecology of invasive plants: state of the art. In H. A. Mooney, R. N. Mack, J. A. McNeely, L. E. Neville, P. J. Schei, and J. K. Waage [eds.], *Invasive alien species: a new synthesis*, 104–161. Island Press, Washington, D.C., USA.
- REJMÁNEK, M., D. M. RICHARDSON, AND P. PYŠEK. 2005b. Plant invasions

- and invasibility of plant communities. In E. Van der Maarel [ed.], *Vegetation ecology*, 332–355. Blackwell, Malden, Massachusetts, USA.
- RICHARDSON, D. M., AND M. REJMÁNEK. 2004. Conifers as invasive aliens: a global survey and predictive framework. *Diversity and Distributions* 10: 321–331.
- ROCHÉ, B. F., C. T. ROCHÉ, AND R. C. CHAPMAN. 1994. Impacts of grassland habitat on yellow starthistle (*Centaurea solstitialis* L.) invasion. *Northwest Science* 68: 86–96.
- SAS. 1998. StatView 5.0.1 reference. SAS Institute, Cary, North Carolina, USA.
- SAUNDERS, C. F. 1926. *Trees and shrubs of California gardens*. Robert M. McBride, New York, New York, USA.
- SAVERIMUTTU, T., AND M. WESTOBY. 1996. Components of variation in seedling potential relative growth rate: phylogenetically independent contrasts. *Oecologia* 105: 281–285.
- SHEA, K., AND P. CHESSON. 2002. Community theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17: 170–176.
- SHIPLEY, B. 2006. Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Functional Ecology* 20: 565–574.
- SIMBERLOFF, D. 2005. Non-native species do threaten the natural environment! *Journal of Agricultural and Environmental Ethics* 18: 595–607.
- VITOUSEK, P. M. 2004. *Nutrient cycling and limitation. Hawaii as a model system*. Princeton University Press, Princeton, New Jersey, USA.
- VITOUSEK, P. M., J. ABER, R. W. HOWARTH, G. E. LIKENS, P. A. MATSON, D. W. SCHINDLER, W. H. SCHESLINGER, AND G. D. TILMAN. 1997. Human alteration of the global nitrogen cycle: causes and consequences. *Issues in Ecology* 1: 2–15.
- WEBER, E. 2003. *Invasive plant species of the world: a reference guide to environmental weeds*. CABI Publishing, Oxon, UK.
- WESTOBY, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.
- WIDRLECHNER, M. P., J. R. THOMPSON, J. K. ILES, AND P. M. DIXON. 2004. Models for predicting the risk of naturalization of non-native woody plants in Iowa. *Journal of Environmental Horticulture* 22: 23–31.
- WILSON, A. 1938. *Distinctive trees, shrubs, and vines in the gardens of the San Francisco peninsula*. Happy Hours, Menlo Park, California, USA.
- WOJCIECHOWSKI, M. F., M. LAVIN, AND M. J. SANDERSON. 2004. A phylogeny of legumes (Leguminosae) based on analysis of the plastid *matK* gene resolves many well-supported subclades within the family. *American Journal of Botany* 91: 1846–1862.
- WRIGHT, I. J., P. B. REICH, M. WESTOBY, D. D. ACKERLY, Z. BARUCH, F. BONGERS, J. CAVENDER-BARES, T. CHAPIN, J. H. C. CORNELISSEN, M. DIEMER, J. FLEXAS, E. GARNIER, P. K. GROOM, J. GULIAS, K. HIKOSAKA, B. B. LAMONT, T. LEE, W. LEE, C. LUSK, J. J. MIDGLEY, M. L. NAVAS, U. NIINEMETS, J. OLEKSYN, N. OSADA, H. POORTER, P. POOT, L. PRIOR, V. I. PYANKOV, C. ROUMET, S. C. THOMAS, M. G. TJOELKER, E. J. VENEKLAAS, AND R. VILLAR. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- ZAVALETA, E. 2000. Valuing ecosystem services lost to *Tamarix* invasion in the United States. In H. A. Mooney and R. J. Hobbs [eds.], *Invasive species in a changing world*, 261–300. Island Press, Washington, D.C., USA.